Smilodon

Smilodon is a genus of the extinct machairodont subfamily of the felids. It is one of the most famous prehistoric mammals and the best known saber-toothed cat. Although commonly known as the **saber-toothed tiger**, it was not closely related to the tiger or other modern cats. *Smilodon* lived in the Americas during the Pleistocene epoch (2.5 mya – 10,000 years ago). The genus was named in 1842 based on fossils from Brazil; the generic name means "scalpel" or "two-edged knife" combined with "tooth". Three species are recognized today: ***S. gracilis***, ***S. fatalis***, and ***S. populator***. The two latter species were probably descended from *S. gracilis*, which itself probably evolved from *Megantereon*. The hundreds of individuals obtained from the La Brea Tar Pits in Los Angeles constitute the largest collection of *Smilodon* fossils.

Overall, *Smilodon* was more robustly built than any extant cat, with particularly well-developed forelimbs and exceptionally long upper canine teeth. Its jaw had a bigger gape than that of modern cats, and its upper canines were slender and fragile, being adapted for precision killing. *S. gracilis* was the smallest species at 55 to 100 kg (120 to 220 lb) in weight. *S. fatalis* had a weight of 160 to 280 kg (350 to 620 lb) and height of 100 cm (39 in). Both of these species are mainly known from North America, but remains from South America have also been attributed to them. *S. populator* from South America was the largest species, at 220 to 436 kg (485 to 961 lb) in weight and 120 cm (47 in) in height, and was among the largest known felids. The coat pattern of *Smilodon* is unknown, but it has been artistically restored with plain or spotted patterns.

In North America, *Smilodon* hunted large herbivores such as bison and camels, and it remained successful even when encountering new prey species in South America. *Smilodon* is thought to have killed its prey by holding it still with its forelimbs and biting it, but it is unclear in what manner the bite itself was delivered. Scientists debate whether *Smilodon* had a social or a solitary lifestyle; analysis of modern predator behavior as well as of *Smilodon*'s fossil remains could be construed to lend support to either view. *Smilodon* probably lived in closed habitats such as forests and bush, which would have provided cover for ambushing prey. *Smilodon* died out at the same time that most North and South American megafauna disappeared, about 10,000 years ago. Its reliance on large animals has been proposed as the cause of its extinction, along with climate change and competition with other species, but the exact cause is unknown.

Smilodon
Temporal range: Early Pleistocene to Early Holocene, 2.5–0.01 Ma
Pre€ € O S D C P T J K PgN

S. fatalis skeleton at National Museum of Natural History, Washington, D.C.
Scientific classification
Kingdom: Animalia
Phylum: Chordata
Class: Mammalia
Order: Carnivora
Suborder: Feliformia
Family: Felidae
Subfamily: †Machairodontinae
Tribe: †Smilodontini
Genus: †*Smilodon* Lund, 1842
Type species
†***Smilodon populator*** Lund, 1842
Other species
▪ †***S. fatalis*** Leidy, 1869
▪ †***S. gracilis*** Cope, 1880
Synonyms

Contents

Taxonomy

S. populator skull and syntype canine from Lund's collection, Zoological Museum, Copenhagen

During the 1830s, Danish naturalist Peter Wilhelm Lund and his assistants collected fossils in the calcareous caves near the small town of Lagoa Santa, Minas Gerais, Brazil. Among the thousands of fossils found, he recognized a few isolated cheek teeth as belonging to a hyena, which he named *Hyaena neogaea* in 1839. After more material was found (including canine teeth and foot bones), Lund concluded the fossils instead belonged to a distinct genus of felid, though transitional to the hyenas. He stated it would have matched the largest modern predators in size, and was more robust than any modern cat. Lund originally wanted to name the new genus *Hyaenodon*, but realizing this had recently become preoccupied by another prehistoric predator, he instead named it *Smilodon populator* in 1842. He explained the Ancient Greek meaning of *Smilodon* as σμίλη (*smilē*), "scalpel" or "two-edged knife", and *οδόντος* (*odontús*), "tooth". This has also been translated as "tooth shaped like double-edged knife". He explained the species name *populator* as "the destroyer", which has also been translated as "he who brings devastation". By 1846, Lund had acquired nearly every part of the skeleton (from different

Genus synonymy

- *Munifelis* Muñis, 1845
- *Trucifelis* Leidy, 1868
- *Smilodontopsis* Brown, 1908
- *Prosmilodon* Rusconi, 1929
- *Smilodontidion* Kraglievich, 1948

Species synonymy

- ***S. populator*:**
  - *Munifelis bonaerensis* Muñis, 1845
  - *Smilodon blainvillii* Desmarest, 1860
  - *Machaerodus bonaerensis* Burmeister, 1867
  - *Machaerodus necator* Gervais, 1878
  - *Smilodon ensenadensis* Ameghino, 1888
  - *Machaerodus ensenadensis* Ameghino, 1889
  - *Smilodon crucians* Ameghino, 1904
  - *Smilodon bonaerensis* Ameghino, 1907
  - *Smilodon neogaeus ensenadensis* Boule & Thévenin, 1920
  - *Smilodon* (*Prosmilodon*) *ensenadensis* Rusconi, 1929
  - *Smilodon neogaeus* de Paula Couto, 1940
  - *Smilodon necator* de Paula Couto, 1940

individuals), and more specimens were found in neighboring countries by other collectors in the following years.[1][2] Though some later authors used Lund's original species name *neogaea* instead of *populator*, it is now considered an invalid *nomen nudum* ("naked name"), as it was not accompanied with a proper description and no type specimens were designated.[3] Some South American specimens have been referred to other genera, subgenera, species, and subspecies, such as *Smilodontidion riggii*, *Smilodon* (*Prosmilodon*) *ensenadensis*, and *S. bonaeriensis*, but these are now thought to be junior synonyms of *S. populator*.[4]

Fossils of *Smilodon* were discovered in North America from the second half of the 19th century onwards.[1] In 1869, American paleontologist Joseph Leidy described a maxilla fragment with a molar, which had been discovered in a petroleum bed in Hardin County, Texas. He referred the specimen to the genus *Felis* (which was then used for most cats, extant as well as extinct) but found it distinct enough to be part of its own subgenus, as *F.* (*Trucifelis*) *fatalis*.[5] The species name means "fate" or "destiny", but it is thought Leidy intended it to mean "fatal".[6] In an 1880 article about extinct American cats, American paleontologist Edward Drinker Cope pointed out that the *F. fatalis* molar was identical to that of *Smilodon*, and he proposed the new combination *S. fatalis*.[7] Most North American finds were scanty until excavations began in the La Brea Tar Pits in Los Angeles, where hundreds of individuals of *S. fatalis* have been found since 1875.[1] *S. fatalis* has junior synonyms such as *S. mercerii*, *S. floridanus*, and *S. californicus*.[4] American paleontologist Annalisa Berta considered the holotype of *S. fatalis* too incomplete to be an adequate type specimen, and the species has at times been proposed to be a junior synonym of *S. populator*.[3] Swedish paleontologists Björn Kurtén and Lars Werdelin supported the distinctness of the two species in 1990.[8]

In his 1880 article about extinct cats, Cope also named a third species of *Smilodon*, *S. gracilis*. The species was based on a partial canine, which had been obtained in a cave near the Schuylkill River in Pennsylvania. Cope found the canine to be distinct from that of the other *Smilodon* species due to its smaller size and more compressed base.[7] Its specific name refers to the species' lighter build.[9] This species is known from fewer and less complete remains than the other members of the genus.[10] *S. gracilis* has at times been considered part of genera such as *Megantereon* and *Ischyrosmilus*.[11] *S. populator*, *S. fatalis* and *S. gracilis* are currently considered the only valid species of *Smilodon*, and features used to define most of their junior synonyms have been dismissed as variation between individuals of the same species (intraspecific variation).[4][3] One of the most famous of prehistoric mammals, *Smilodon* has often been featured in popular media and is the state fossil of California.[1]

Evolution

- *Smilodon* (*Prosmilodon*) *ensenadensis ferox* Kraglievich, 1947
- *Smilodon* (*Prosmilodon*) *ensenadensis minor* Kraglievich, 1948
- *Smilodontidion riggii* Kraglievich, 1948
- *Machaerodus neogaeus* Pictet, 1953
- *Felis smilodon* Desmarest, 1953
- *Smilodon populator populator* de Paula Couto, 1955

- ***S. fatalis*:**
  - *Felis* (*Trucifelis*) *fatalis* Leidy, 1868
  - *Trucifelis fatalis* Leidy, 1869
  - *Machaerodus fatalis* Lydekker, 1884
  - *Drepanodon floridanus* Leidy, 1889
  - *Machaerodus floridanus* Leidy, 1889
  - *Uncia mercerii* Cope, 1895
  - *Smilodon floridanus* Adams, 1896
  - *Machaerodus* (*Smilodon*) *mercerii* Cope, 1899
  - *Smilodon californicus* Bovard, 1907
  - *Smilodontopsis troglodytes* Brown, 1908
  - *Smilodontopsis conardi* Brown, 1908

Long the most completely known saber-toothed cat, *Smilodon* is still one of the best-known members of the group, to the point where the two concepts have been confused. The term "saber-tooth" refers to an ecomorph consisting of various groups of extinct predatory synapsids (mammals and close relatives), which convergently evolved extremely long maxillary canines, as well as adaptations to the skull and skeleton related to their use. This includes members of Gorgonopsia, Thylacosmilidae, Machaeroidinae, Nimravidae, Barbourofelidae, and Machairodontinae.[1][12] Within the family Felidae (true cats), members of the subfamily Machairodontinae are referred to as saber-toothed cats, and this group is itself divided into three tribes: Metailurini (false saber-tooths); Homotherini (scimitar-toothed cats); and Smilodontini (dirk-toothed cats), to which *Smilodon* belongs.[4] Members of Smilodontini are defined by their long slender canines with fine to no serrations, whereas Homotherini are typified by shorter, broad, and more flattened canines, with coarser serrations.[13] Members of Metailurini were less specialized and had shorter, less flattened canines, and are not recognized as members of Machairodontinae by some researchers.[4]

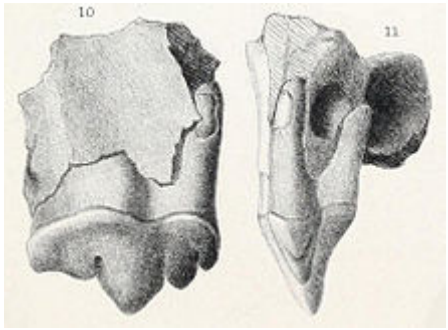
The earliest felids are known from the Oligocene of Europe, such as *Proailurus*, and the earliest one with saber-tooth features is the Miocene genus *Pseudaelurus*.[4] The skull and mandible morphology of the earliest saber-toothed cats was similar to that of the modern clouded leopards (*Neofelis*). The lineage further adapted to the precision killing of large animals by developing elongated canine teeth and wider gapes, in the process sacrificing high bite force.[14] As their canines became longer, the bodies of the cats became more robust for immobilizing prey.[13] In derived smilodontins and homotherins, the lumbar region of the spine and the tail became shortened, as did the hind limbs.[4] Based on mitochondrial DNA sequences extracted from fossils, the lineages of *Homotherium* and *Smilodon* are estimated to have diverged about 18 Ma ago.[15] The earliest species of *Smilodon* is *S. gracilis*, which existed from 2.5 million to 500,000 years ago (early Blancan to Irvingtonian ages) and was the successor in North America of *Megantereon*, from which it probably evolved. *Megantereon* itself had entered North America from Eurasia during the Pliocene, along with *Homotherium*. *S. gracilis* reached the northern regions of South America in the Early Pleistocene as part of the Great American Interchange.[16][13] The younger *Smilodon* species are probably derived from *S. gracilis*.[17] *S. fatalis* existed 1.6 million–10,000 years ago (late Irvingtonian to Rancholabrean ages), and replaced *S. gracilis* in North America.[8] *S. populator* existed 1 million–10,000 years ago (Ensenadan to Lujanian ages); it occurred in the eastern parts of South America.[18]

- *Smilodontopsis mercerii* Brown, 1908
- *Smilodon nebraskensis* Matthew, 1918
- *Machaerodus mercerii* Matthew, 1918
- *Smilodon* (*Trucifelis*) *californicus* Merriam & Stock, 1932
- *Smilodon* (*Trucifelis*) *fatalis* Merriam & Stock, 1932
- *Smilodon* (*Trucifelis*) *nebraskensis* Merriam & Stock, 1932
- *Smilodon* (*Trucifelis*) *californicus brevipes* Merriam & Stock, 1932
- *Smilodon* trinitensis *Slaughter, 1960*

- ***S. gracilis*:**
  - *Machaerodus* (*Smilodon*) *gracilis* Cope, 1899
  - *Smilodon* (*Smilodontopsis*) *gracilis* Merriam & Stock, 1932
  - *Megantereon gracilis* Broom & Schepers 1946
  - *Ischyrosmilus gracilis* Churcher, 1984
  - *Smilodontopsis gracilis* Berta, 1995

Despite the colloquial name "saber-toothed tiger", *Smilodon* is not closely related to the modern tiger (which belongs in the subfamily Pantherinae), or any other extant felid.[19] A 1992 ancient DNA analysis suggested that *Smilodon* should be grouped with modern cats (subfamilies Felinae and Pantherinae).[20] A 2005 study found that *Smilodon* belonged to a separate lineage.[21] A study published in 2006 confirmed this, showing that the Machairodontinae diverged early from the ancestors of modern cats and were not closely related to any

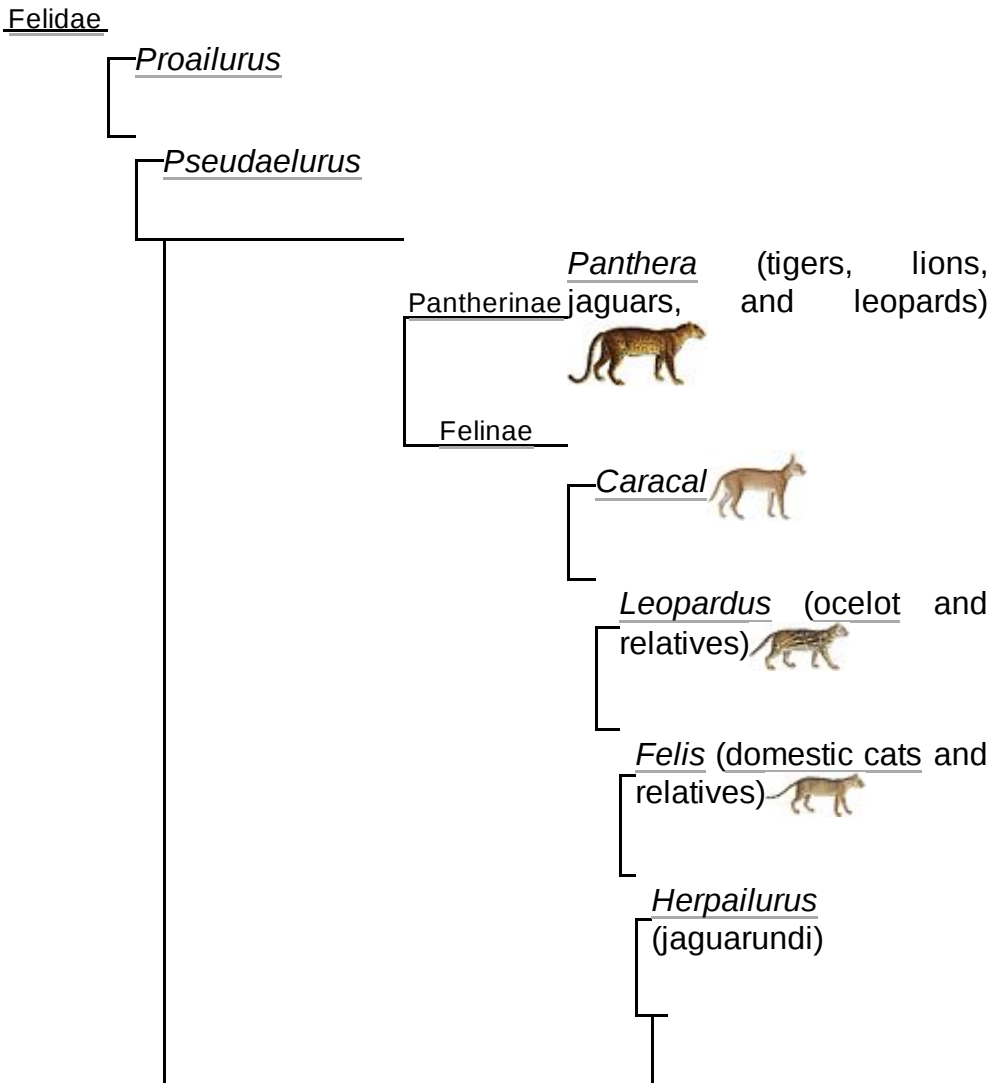
living species.[22] The following cladogram based on fossils and DNA analysis shows the placement of *Smilodon* among extinct and extant felids, after Rincón and colleagues, 2011:[16]



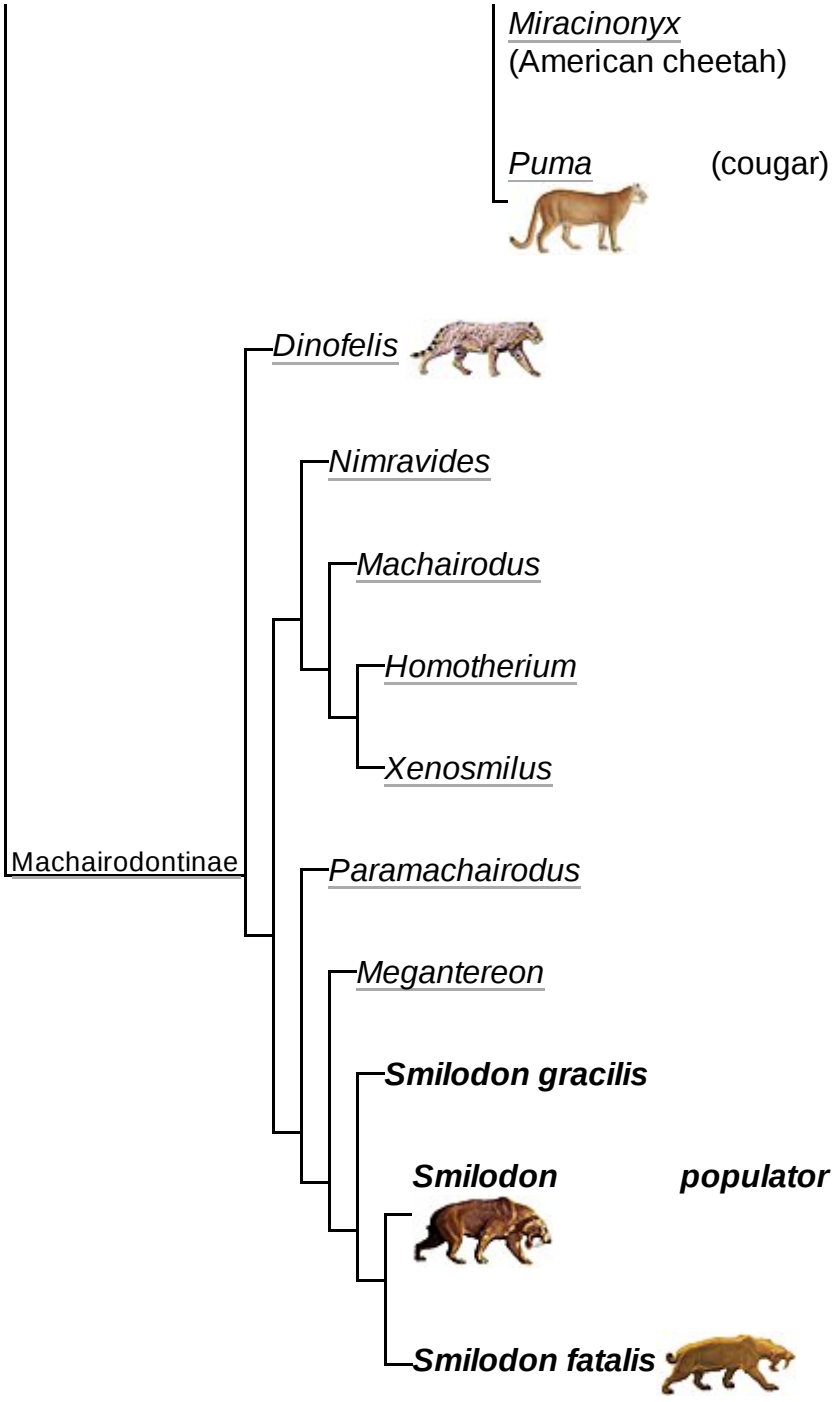
1869 lithograph of the holotype molar and maxilla fragment of *S. fatalis*


S. populator canine tooth; the tip points to the right

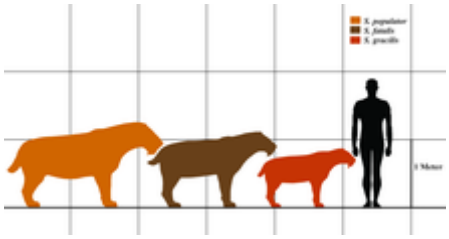

S. populator skeleton, Museo de La Plata, Buenos Aires




S. populator statue in Tierpark Berlin, Erich Oehme, 1964



Description



Size of the three *Smilodon* species compared to a human

Smilodon was around the size of modern big cats, but was more robustly built. It had a reduced lumbar region, high scapula, short tail, and broad limbs with relatively short feet.[23][24] *Smilodon* is most famous for its relatively long canine teeth, which are the longest found in the saber-toothed cats, at about 28 cm (11 in) long in the largest species, *S. populator*.[23] The canines were slender and had fine serrations on the front and back side.[25] The skull was robustly proportioned and the muzzle was short and broad. The cheek bones (zygomata) were deep and widely arched, the sagittal crest was prominent, and the frontal region was slightly convex. The mandible had a flange on each side of the front. The upper incisors were large, sharp, and slanted forwards. There was a

diastema (gap) between the incisors and molars of the mandible. The lower incisors were broad, recurved, and placed in a straight line across. The p3 premolar tooth of the mandible was present in most early specimens, but lost in later specimens; it was only present in 6% of the La Brea sample.[3] There is some dispute over whether *Smilodon* was sexually dimorphic. Some studies of *S. fatalis* fossils have found little difference between the sexes.[26][27] Conversely, a 2012 study found that, while fossils of *S. fatalis* show less variation in size among individuals than modern *Panthera*, they do appear to show the same difference between the sexes in some traits.[28]

S. populator restored with plain coat, Charles R. Knight, 1903

S. gracilis was the smallest species, estimated at 55 to 100 kg (120 to 220 lb) in weight, about the size of a jaguar. It was similar to its predecessor *Megantereon* of the same size, but its dentition and skull were more advanced, approaching *S. fatalis*.[29][4] *S. fatalis* was intermediate in size between *S. gracilis* and *S. populator*.[23] It ranged from 160 to 280 kg (350 to 620 lb).[29] and reached a shoulder height of 100 cm (39 in) and body length of 175 cm (69 in).[30] It was similar to a lion in dimensions, but was more robust and muscular, and therefore had a larger body mass. Its skull was also similar to that of *Megantereon*, though more massive and with larger canines.[4] *S. populator* was among the largest known felids, with a body mass range of 220 to 400 kg (490 to 880 lb),[29] and one estimate suggesting up to 470 kg (1,040 lb).[31] A particularly large *S. populator* skull from Uruguay measuring 39 cm (15 in) in length indicates this individual may have weighed as much as 436 kg (961 lb).[32] It stood at a shoulder height of 120 cm (47 in).[23] Compared to *S. fatalis*, *S. populator* was more robust and had a more elongated and narrow skull with a straighter upper profile, higher positioned nasal bones, a more vertical occiput, more massive metapodials and slightly longer forelimbs relative to hindlimbs.[4][8] Large tracks from Argentina (for which the ichnotaxon name *Smilodonichium* has been proposed) have been attributed to *S. populator*, and measure 17.6 cm (6.9 in) by 19.2 cm (7.6 in).[33] This is larger than tracks of the Bengal tiger, to which the footprints have been compared.[34]

S. fatalis restored with spotted coat

Traditionally, saber-toothed cats have been artistically restored with external features similar to those of extant felids, by artists such as Charles R. Knight in collaboration with various paleontologists in the early 20th century.[35] In 1969, paleontologist G. J. Miller instead proposed that *Smilodon* would have looked very different from a typical cat and similar to a bulldog, with a lower lip line (to allow its mouth to open wide without tearing the facial tissues), a more retracted nose and lower-placed ears.[36] Paleoartist Mauricio Antón and coauthors disputed this in 1998 and maintained that the facial features of *Smilodon* were overall not very different from those of other cats. Antón noted that modern animals like the hippopotamus are able to achieve a wide gap without tearing tissue by the moderate folding of the orbicularis oris muscle, and such a muscle configuration exists in modern large felids.[37] Antón stated that extant phylogenetic bracketing (where the features of the closest extant relatives of a fossil taxon are used as reference) is the most reliable way of restoring the life-appearance of prehistoric animals, and the cat-like *Smilodon* restorations by Knight are therefore still accurate.[35]

Smilodon and other saber-toothed cats have been reconstructed with both plain-colored coats and with spotted patterns (which appears to be the ancestral condition for feliforms), both of which are considered possible.[35] Studies of modern cat species have found that species that live in the open tend to have uniform coats while those that live in more vegetated habitats have more markings, with some exceptions.[38] Some coat features, such as the manes of male lions or the stripes of the tiger, are too unusual to predict from fossils.[35]

Paleobiology

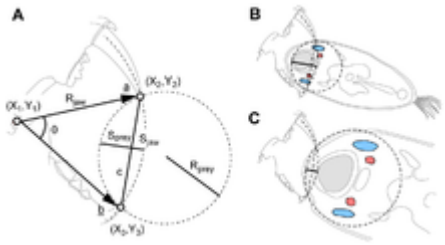
Predatory behavior

S. fatalis fighting dire wolves over a Columbian mammoth carcass in the La Brea Tar Pits, Robert Bruce Horsfall, 1913

An apex predator, *Smilodon* primarily hunted large mammals. Isotopes preserved in the bones of *S. fatalis* in the La Brea Tar Pits reveal that ruminants like bison (*Bison antiquus*, which was much larger than the modern American bison) and camels (*Camelops*) were most commonly taken by the cats there.[39] In addition, isotopes preserved in the tooth enamel of *S. gracilis* specimens from Florida show that this species fed on the peccary *Platygonus* and the llama-like *Hemiauchenia*.[40] In rare cases, *Smilodon* may have also targeted glyptodonts, based on a *Glyptotherium* skull that bears elliptical puncture marks[41] consistent with the size and diameter of its canine teeth.[42] This was a juvenile glyptodont with an incompletely developed cephalic shield (head armor).[41] Isotopic studies of dire wolf (*Canis dirus*) and American lion (*Panthera atrox*) bones show an overlap with *S. fatalis* in prey, which suggests that they were competitors.[39] More detailed isotope analysis however, indicates that *Smilodon fatalis* preferred forest-dwelling prey such as tapirs, deer and forest-dwelling bison as opposed to the dire wolves' preferences for prey inhabiting open areas such grassland.[43] The availability of prey in the Rancho La Brea area was likely comparable to modern East Africa.[44] As *Smilodon* migrated to South America, its diet changed; bison were absent, the horses and proboscideans were different, and native ungulates such as toxodonts and litopterns were completely unfamiliar, yet *S. populator* thrived as well there as its relatives in North America.[13] Isotopic analysis for *Smilodon populator* suggests that its main prey species included *Toxodon platensis*, *Pachyarmatherium*, *Holmesina*, species of the genus *Panochthus*, *Palaeolama*, *Catonyx*, *Equus neogeus*, and the crocodilian *Caiman latirostris*. This analysis of its diet also indicates that *S. populator* hunted both in open and forested habitats.[45] The differences between the North and South American species may be due to the difference in prey between the two continents.[8] *Smilodon* probably avoided eating bone and would have left enough food for scavengers.[46] *Smilodon* itself may have scavenged dire wolf kills.[47] It has been suggested that *Smilodon* was a pure scavenger that used its canines for display to assert dominance over carcasses, but this theory is not supported today as no modern terrestrial mammals are pure scavengers.[48]

The brain of *Smilodon* had sulcal patterns similar to modern cats, which suggests an increased complexity of the regions that control the sense of hearing, sight, and coordination of the limbs. Felid saber-tooths in general had relatively small eyes that were not as forward-facing as those of modern cats, which have good binocular vision to help them move in trees.[48] *Smilodon* was likely an ambush predator that concealed itself in dense vegetation, as its limb proportions were similar to modern forest dwelling cats,[49] and its short tail would not have helped it balance while running.[50] Unlike its ancestor *Megantereon*, which was at least partially scansorial and therefore able to climb trees, *Smilodon* was probably completely terrestrial due to its greater weight and lack of climbing adaptations.[51] The heel bone of *Smilodon* was fairly long, which suggests it was a good jumper.[23] Its well-developed flexor and extensor muscles in its forearms probably enabled it to pull down, and securely hold down, large prey. Analysis of the cross-sections of *S. fatalis* humeri indicated that they were strengthened by cortical thickening to such an extent that they would have been able to sustain greater loading than those of extant big cats, or of the extinct American lion. The thickening of *S. fatalis* femurs was within the range of extant felids.[52] Its canines were fragile and could not have bitten into bone; due to the risk of breaking, these cats had to subdue and restrain their prey with their powerful forelimbs before they could use their canine teeth, and likely used quick slashing or stabbing bites rather than the slow,

suffocating bites typically used by modern cats.[52] On rare occasions, as evidenced by fossils, *Smilodon* was willing to risk biting into bone with its canines. This may have been focused more towards competition such as other *Smilodon* or potential threats such as other carnivores than on prey.[51]



Maximum gape (A) and reconstructions of neck bite in prey of different sizes (B, C)

Debate continues as to how *Smilodon* killed its prey. Traditionally, the most popular theory is that the cat delivered a deep stabbing bite or open-jawed stabbing thrust to the throat, killing the prey very quickly.[52][53] Another hypothesis suggests that *Smilodon* targeted the belly of its prey. This is disputed, as the curvature of their prey's belly would likely have prevented the cat from getting a good bite or stab.[54] In regard to how *Smilodon* delivered its bite, the "canine shear-bite" hypothesis has been favored, where flexion of the neck and rotation of the skull assisted in biting the prey, but this may be mechanically impossible. The mandibular flanges may have helped resist bending forces when the mandible was pulled against the hide of a prey.[55] The protruding incisors were arranged in an arch, and were used to hold the prey still and stabilize it while the canine bite was delivered. The contact surface between the canine crown and the gum was enlarged, which helped stabilize the tooth and helped the cat sense when the tooth had penetrated to its maximum extent. Since saber-toothed cats generally had a relatively large infraorbital foramen (opening) in the skull, which housed nerves associated with the whiskers, it has been suggested the improved senses would have helped the cats' precision when biting outside their field of vision, and thereby prevent breakage of the canines. The blade-like carnassial teeth were used to cut skin to access the meat, and the reduced molars suggest that they were less adapted for crushing bones than modern cats.[48] As the food of modern cats enters the mouth through the side while cutting with the carnassials, not the front incisors between the canines, the animals do not need to gape widely, so the canines of *Smilodon* would likewise not have been a hindrance when feeding.[37]


La Brea *S. fatalis* skull cast with jaws at maximum gape

Despite being more powerfully built than other large cats, *Smilodon* had a weaker bite. Modern big cats have more pronounced zygomatic arches, while these were smaller in *Smilodon*, which restricted the thickness and therefore power of the temporalis muscles and thus reduced *Smilodon*'s bite force. Analysis of its narrow jaws indicates that it could produce a bite only a third as strong as that of a lion (the bite force quotient measured for the lion is 112).[56][57] There seems to be a general rule that the saber-toothed cats with the largest canines had proportionally weaker bites. Analyses of canine bending strength (the ability of the canine teeth to resist bending forces without breaking) and bite forces indicate that the saber-toothed cats' teeth were stronger relative to the bite force than those of modern big cats.[58] In addition, *Smilodon*'s gape could have reached almost 120 degrees,[59] while that of the modern lion reaches 65 degrees.[60] This made the gape wide enough to allow *Smilodon* to grasp large prey despite the long canines.[37] A 2018 study compared the killing behavior of *Smilodon fatalis* and *Homotherium serum*, and found that the former had a strong skull with little trabecular bone for a stabbing canine-shear bite, whereas the latter had more trabecular bone and used a clamp and hold style more similar to lions. The two would therefore have held distinct ecological niches.[61]

Natural traps

Mounted skeletons of *S. fatalis* and a dire wolf near mired *Paramylodon*

Many *Smilodon* specimens have been excavated from asphalt seeps that acted as natural carnivore traps. Animals were accidentally trapped in the seeps and became bait for predators that came to scavenge, but these were then trapped themselves. The best-known of such traps are at La Brea in Los Angeles, which have produced over 166,000 *Smilodon fatalis* specimens[62] that form the largest collection in the world. The sediments of the pits there were accumulated 40,000 to 10,000 years ago, in the Late Pleistocene. Though the trapped animals were buried quickly, predators often managed to remove limb bones from them, but they were themselves often trapped and then scavenged by other predators; 90% of the excavated bones belonged to predators.[63]

The Talara Tar Seeps in Peru represent a similar scenario, and have also produced fossils of *Smilodon*. Unlike in La Brea, many of the bones were broken or show signs of weathering. This may have been because the layers were shallower, so the thrashing of trapped animals damaged the bones of previously trapped animals. Many of the carnivores at Talara were juveniles, possibly indicating that inexperienced and less fit animals had a greater chance of being trapped. Though Lund thought accumulations of *Smilodon* and herbivore fossils in the Lagoa Santa Caves were due to the cats using the caves as dens, these are probably the result of animals dying on the surface, and water currents subsequently dragging their bones to the floor of the cave, but some individuals may also have died after becoming lost in the caves.[63]

Social life

S. fatalis pair approaching a group of *Paramylodon*, one mired, at the La Brea Tar Pits, Charles R. Knight, 1921

Scientists debate whether *Smilodon* was social. One study of African predators found that social predators like lions and spotted hyenas respond more to the distress calls of prey than solitary species. Since *S. fatalis* fossils are common at the La Brea Tar Pits, and were likely attracted by the distress calls of stuck prey, this could mean that this species was social as well.[64] One critical study claims that the study neglects other factors, such as body mass (heavier animals are more likely to get stuck than lighter ones), intelligence (some social animals, like the American lion, may have avoided the tar because they were better able to recognize the hazard), lack of visual and olfactory lures, the type of audio lure, and the length of the distress calls (the actual distress calls of the trapped prey animals would have lasted longer than the calls used in the study). The author of that study ponders what predators would have responded if the recordings were played in India, where the otherwise solitary tigers are known to aggregate around a single carcass.[65] The authors of the original study responded that though effects of the calls in the tar pits and the playback experiments would not be identical, this would not be enough to overturn their conclusions. In addition, they stated that weight and intelligence would not likely affect the results as lighter carnivores are far more numerous than heavy herbivores and the social (and seemingly intelligent) dire wolf is also found in the pits.[66] The structure of the hyoid bones suggest that *Smilodon* communicated by roaring, like modern big cats.[67] The ability to roar may have implications for their social life.[68]

Another argument for sociality is based on the healed injuries in several *Smilodon* fossils, which would suggest that the animals needed others to provide it food.[69] This argument has been questioned, as cats can recover quickly from even severe bone damage and an injured *Smilodon* could survive if it had access to water.[70] The brain of *Smilodon* was relatively small compared to other cat species. Some researchers have argued that *Smilodon*'s brain would have been too small for it to have been a social animal.[71] An analysis of brain size in living big cats found no correlation between brain size and sociality.[72] Another argument against *Smilodon* being social is that being an ambush hunter in closed habitat would likely have made group-living

Lion pride attacking an African buffalo in Tanzania; *Smilodon* may also have hunted in groups

unnecessary, as in most modern cats.[70] Yet it has also been proposed that being the largest predator in an environment comparable to the savanna of Africa, *Smilodon* may have had a social structure similar to modern lions, which possibly live in groups primarily to defend optimal territory from other lions (lions are the only social big cats today).[48]

Whether *Smilodon* was sexually dimorphic has implications for its reproductive behavior. Based on their conclusions that *Smilodon fatalis* had no sexual dimorphism, Van Valkenburgh and Sacco suggested in 2002 that, if the cats were social, they would likely have lived in monogamous pairs (along with offspring) with no intense competition among males for females.[26] Likewise, Meachen-Samuels and Binder (2010) concluded that aggression between males was less pronounced in *S. fatalis* than in the American lion.[27] Christiansen and Harris (2012) found that, as *S. fatalis* did exhibit some sexual dimorphism, there would have been evolutionary selection for competition between males.[28] Some bones show evidence of having been bitten by other *Smilodon*, possibly the result of territorial battles, competition for breeding rights or over prey.[48] Two *S. populator* skulls from Argentina show seemingly fatal, unhealed wounds which appear to have been caused by the canines of another *Smilodon* (though it cannot be ruled out they were caused by kicking prey). If caused by intraspecific fighting, it may also indicate that they had social behavior which could lead to death, as seen in some modern felines (as well as indicating that the canines could penetrate bone).[73] It has been suggested that the exaggerated canines of saber-toothed cats evolved for sexual display and competition, but a statistical study of the correlation between canine and body size in *S. populator* found no difference in scaling between body and canine size concluded it was more likely they evolved solely for a predatory function.[74]

Development

Smilodon started developing its adult saber-teeth when the animal turned one-and-a-half years of age, shortly after the completion of the eruption of the cat's baby teeth. Both baby and adult canines would be present side by side in the mouth for an 11-month period, and the muscles used in making the powerful bite were developed at about one-and-a-half years old as well, eight months earlier than in a modern lion. After *Smilodon* turned around 20 months of age, the infant teeth were shed while the adult canines grew at an average growth rate of 7 mm (0.3 in) per month during a 12-month period. They reached their full size at around 3 years of age, later than for modern species of big cat. Juvenile and adolescent *Smilodon* specimens are extremely rare at Rancho La Brea, where the study was performed, indicating that they remained hidden or at denning sites during hunts, and depended on parental care while their canines were developing.[75][76][77]

Undersides of *S. fatalis* skulls, showing canine replacement, George C. Page Museum

A 2017 study indicates that juveniles were born with a robust build similar to the adults. Comparison of the bones of juvenile *S. fatalis* specimens from La Brea with those of the contemporaneous American lion revealed that the two cats shared a similar growth curve. Felid forelimb development during ontogeny (changes during growth) has remained tightly constrained. The curve is similar to that for modern cats such as tigers and cougars, but shifts more towards the robust direction of the axes than is seen in modern felids.[78]

Paleopathology

Several *Smilodon* fossils show signs of ankylosing spondylitis, hyperostosis and trauma;[79] some also had arthritis, which gave them fused vertebrae. One study of 1,000 *Smilodon* skulls found that 30% of them had eroded parietal bones, which is where the largest jaw muscles attach. They also showed signs of microfractures, and the weakening and thinning of bones possibly caused by mechanical stress from the constant need to make stabbing motions with the canines.[80] Bony growths where the deltoid muscle inserted in the humerus is a common pathology for a La Brea specimen, which was probably due to repeated strain when *Smilodon* attempted to pull down prey with its forelimbs. Sternum injuries are also common, probably due to collision with prey.[48] The frequency of trauma in *S. fatalis* specimens was 4.3%, compared to 2.8% in the dire wolf, which implies the ambush predatory behavior of the former led to greater risk of injury than the pursuit predatory behavior of the latter. *Smilodon* remains exhibit relatively more shoulder and lumbar vertebrae injuries.[81]

Distribution and habitat

S. fatalis in climbing posture, Cleveland Museum of Natural History

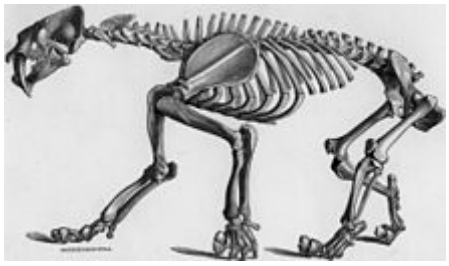
Smilodon lived during the Pleistocene epoch (2.5 mya–10,000 years ago), and was perhaps the most recent of the saber-toothed cats.[23] It probably lived in closed habitat such as forest or bush.[82] Fossils of the genus have been found throughout the Americas.[3] The habitat of North America varied from subtropical forests and savannah in the south, to treeless mammoth steppes in the north. *S. fatalis* fossils have been found as far north as Alberta, Canada.[83] The mosaic vegetation of woods, shrubs, and grasses in southwestern North America supported large herbivores such as horses, bison, antelope, deer, camels, mammoths, mastodons, and ground sloths. North America also supported other saber-toothed cats, such as *Homotherium* and *Xenosmilus*, as well as other large carnivores including dire wolves, short-faced bear (*Arctodus simus*) and the American lion.[13][63][84] Competition from such carnivores may have prevented North American *S. fatalis* from attaining the size of South America's *S. populator*. The similarity in size of *S. fatalis* and the American lion suggests niche overlap and direct competition between these species, and they appear to have fed on similarly sized prey.[85]

S. gracilis entered South America during the early to middle Pleistocene, where it probably gave rise to *S. populator*, which lived in the eastern part of the continent. *S. fatalis* also entered western South America in the late Pleistocene, and the two species were thought to be divided by the Andes mountains.[8][16][23] However, in 2018, a skull of *S. fatalis* found in Uruguay east of the Andes was reported, which puts the idea that the two species were allopatric (geographically separated) into question.[86] The American interchange resulted in a mix of native and invasive species sharing the prairies and woodlands in South America; North American herbivores included proboscideans, horses, camelids and deer, South American herbivores included toxodonts, litopterns, ground sloths, and glyptodonts. Native metatherian predators (including the saber-toothed thylacosmilids) had gone extinct by the Pliocene, and were replaced by North American carnivores such as canids, bears, and large cats.[13]

S. populator was very successful, while *Homotherium* never became widespread in South America. The extinction of the thylacosmilids has been attributed to competition with *Smilodon*, but this is probably incorrect, as they seem to have disappeared before the arrival of the large cats. The phorusrhacid "terror birds" may have dominated the large predator niche in South America until *Smilodon* arrived.[13] *S. populator* may have been able to reach larger size than *S. fatalis* due to a lack of competition in Pleistocene South America; *S. populator* arrived after the extinction of *Arctotherium angustidens*, one of the largest carnivores ever, and could therefore assume the niche of mega-carnivore.[85] *S. populator* preferred large prey from open habitats such as grassland and plains, based on evidence gathered from isotope ratios that determined the animal's diet.

In this way, the South American *Smilodon* species was probably similar to the modern lion. *S. populator* probably competed with the canid *Protocyon* there, but not with the jaguar, which fed primarily on smaller prey.[87][88]

Extinction


1880 skeletal diagram of *S. populator*

Along with most of the Pleistocene megafauna, *Smilodon* became extinct 10,000 years ago in the Quaternary extinction event. Its extinction has been linked to the decline and extinction of large herbivores, which were replaced by smaller and more agile ones like deer. Hence, *Smilodon* could have been too specialized at hunting large prey and may have been unable to adapt.[52] A 2012 study of *Smilodon* tooth wear found no evidence that they were limited by food resources.[89] Other explanations include climate change and competition with humans[89] (who entered the Americas around the time *Smilodon* disappeared), or a combination of several factors, all of which apply to the general Pleistocene extinction event, rather than specifically to the extinction of the saber-toothed cats.[90]

Some early writers theorized that the last saber-toothed cats, *Smilodon* and *Homotherium*, became extinct through competition with the faster and more generalized felids that replaced them. It was even proposed that the saber-toothed predators were inferior to modern cats, as the ever-growing canines were thought to inhibit their owners from feeding properly. Yet fast felids, such as the American lion and the American cheetah, also became extinct during the Late Pleistocene. The fact that saber-teeth evolved many times in unrelated lineages also attests to the success of this feature.[90]

The latest *Smilodon fatalis* specimen recovered from the Rancho La Brea tar pits has been dated to 13,025 years ago.[91] The latest *Smilodon populator* remains found in the cave of Cueva del Medio, near the town of Soria, northeast Última Esperanza Province, Magallanes Region in southern-most Chile have been dated to 10,935–11,209 years ago.[92] The most recent carbon-14 date for *S. fatalis* reported was 10,200 years BP for remains from the First American Cave in 1971;[93] however, the most recent "credible" date has been given as 11,130 BP.[94]

See also

- List of largest carnivorans
- List of largest prehistoric carnivorans
- Megafauna
- Quaternary extinction event

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